

The temporal resolution of flight attitude control in dragonflies and locusts: lessons for the design of flapping-wing MAVs

Project report for AFOSR grant no FA4869-06-1-0059, AOARD #064047

Principal Investigator:

Dr. Gert Stange,
Research School of Biological Sciences,
Australian National University,
Building 46,
Canberra ACT 2000, Australia.

gert.stange@anu.edu.au

Contributors:

Fabian Schmeling, Philipps-Universitaet Marburg, Germany;
Richard Berry, Australian National University;
Gerlinde Lenz, Australian National University.

Summary. In order to identify stability constraints in flapping-winged MAVs, within the context of longitudinal stabilization of flight attitude, the question is examined whether insects are capable of controlling flight attitude at the temporal resolution of a single wing beat. It is found that the phenomenon of phase locking between a periodic light flash as the external pacemaker and the wingbeat of insects is suitable for the examination of the time resolution with which vision contributes to stabilization. In tethered locusts, flying in a wind tunnel with a wingbeat frequency of 22 Hz, phase locking can be readily obtained by a periodic stimulus of UV light. It is suggested that the effect is a by-product of the animal continuously trying to apply corrections. Therefore, in the closed-loop situation of free flight, frequency components of the visual input at or above wing beat rate are also present and must contribute to stability control. The response is mediated by the median ocellus. In dragonflies, with a wingbeat frequency of 50 Hz, the effect is not observed. This suggests that organisms or MAV of the size and wingbeat rate of locusts require active damping by visual inputs, whereas the same is not necessary in smaller systems.

Introduction

Conventional aircraft can be designed such that steady-state aerodynamics apply. Thus, it is possible to construct airframes that are intrinsically stable, achieving attitude control via forces that act on stabilizers separate to the wings. Such stability comes at a price, namely a level of manoeuvrability that is inferior to what is theoretically possible. On the other hand, flapping-winged aircraft without separate stabilizers have the potential to be extremely manoeuvrable but are intrinsically unstable, making it necessary to obtain stability by the use of sensor feedback and active control.

Report Documentation Page			Form Approved OMB No. 0704-0188	
Public reporting burden for the collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing the collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden, to Washington Headquarters Services, Directorate for Information Operations and Reports, 1215 Jefferson Davis Highway, Suite 1204, Arlington VA 22202-4302. Respondents should be aware that notwithstanding any other provision of law, no person shall be subject to a penalty for failing to comply with a collection of information if it does not display a currently valid OMB control number.				
1. REPORT DATE 04 DEC 2007	2. REPORT TYPE Final	3. DATES COVERED 01-09-2006 to 01-09-2007		
4. TITLE AND SUBTITLE The temporal resolution of flight attitude control in dragonflies and locusts: lessons for the design of flapping-wing MAVs		5a. CONTRACT NUMBER FA48690610059		
		5b. GRANT NUMBER		
		5c. PROGRAM ELEMENT NUMBER		
6. AUTHOR(S) Gert Stange		5d. PROJECT NUMBER		
		5e. TASK NUMBER		
		5f. WORK UNIT NUMBER		
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) Australian National University, PO Box 475, Canberra ACT 0200, Australia, AU, N/A		8. PERFORMING ORGANIZATION REPORT NUMBER N/A		
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES) AOARD, UNIT 45002, APO, AP, 96337-5002		10. SPONSOR/MONITOR'S ACRONYM(S) AOARD-064047		
		11. SPONSOR/MONITOR'S REPORT NUMBER(S)		
12. DISTRIBUTION/AVAILABILITY STATEMENT Approved for public release; distribution unlimited				
13. SUPPLEMENTARY NOTES				
14. ABSTRACT In order to identify stability constraints in flapping-winged MAVs, within the context of longitudinal stabilization of flight attitude, the question is examined whether insects are capable of controlling flight attitude at the temporal resolution of a single wing beat. It is found that the phenomenon of phase locking between a periodic light flash and the wingbeat of insects is suitable for the examination of the time resolution with which vision contributes to stabilization. In tethered locusts, flying in a wind tunnel with a wingbeat frequency of 22 Hz, phase locking can be readily obtained by a periodic stimulus of UV light. It is suggested that the effect is a by-product of the animal continuously trying to apply corrections. Therefore, in the closed-loop situation of free flight, frequency components of the visual input at or above wing beat rate are also present and must contribute to stability control. The response is mediated by the median ocellus. In dragonflies, with a wingbeat frequency of 50 Hz, the effect is not observed. This suggests that organisms or MAV of the size and wingbeat rate of locusts require active damping by visual inputs, whereas the same is not necessary in smaller systems.				
15. SUBJECT TERMS				
16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT Same as Report (SAR)	18. NUMBER OF PAGES 15
a. REPORT unclassified	b. ABSTRACT unclassified	c. THIS PAGE unclassified		

The present project emerged out of the consideration that insects have resolved a technical challenge that is quite relevant to flapping-wing MAVs, namely a temporal resolution of attitude sensor systems that is adequate for the maintenance of stability. Although some attempts have been made to design sensor fed controllers for flapping wing MAVs, these designs have relied on averaging theory which assumes that the free dynamics of the MAV occur on a much slower time scale than the wing beat frequency. There is evidence that this is not valid for some insects such as locusts and the question arises as to whether it would ever be a valid assumption for small size MAVs, where Reynolds numbers are so low that unsteady lift-generating mechanisms such as vortex capture at individual wing beat rates become important.

The main component of the present project examines the role of visual inputs for the maintenance of longitudinal stability in locusts. Locust flight patterns are predominantly comprised of steady, long-haul forward flight. Yet, their airframes are not intrinsically longitudinally stable like conventional aircraft (THOMAS and TAYLOR, 2003). This suggests that even though their demands on manoeuvrability may be low, intrinsic stability is of no advantage for fliers of this size. Thomas and Taylor, for example, have demonstrated that a natural longitudinal vibration mode of the locust body occurs at 10 Hz, which is of the same order of magnitude as the wing beat frequency (22 Hz). These authors conclude that, due to the added difficulties produced by coupling between wingbeat frequencies and the natural mode of the locust, the close proximity of these frequencies makes it necessary for locusts to control their flight at the resolution of a single wingbeat. They also conclude that coupling between these modes must be prevented by active control.

Earlier work on locusts showed that the sensors involved in active control are visual (compound eyes and ocelli) and mechanoreceptive (wind sensors on head and antennae, force sensors on wing bases). A study on the influence of ocellar mediated inputs on the locust flight motor system has shown that the ocelli mediate fast direct connections with the flight motor neurons and slower indirect connections through interneurons (REICHERT and ROWELL, 1985). However, it is not clear what the transfer properties of these connections are when the ocellus is shown realistic light sequences. Identifying these properties would reveal how the flight motor control system of locusts achieves the damping of the natural longitudinal vibrations required for stability, and how it achieves the temporal resolution of this control system.

A secondary project component addresses the question as to whether visual inputs can also affect longitudinal stability in dragonflies. While the locust may be considered an analog of the C-130, there are no flying machines that match the extraordinary versatility of dragonflies. For example, dragonflies are able to decelerate and accelerate at 10 g, and to achieve 90° turns within 2-3 wing beats (<50 ms.) Our lab has recently discovered that dragonflies have evolved an ocellar system that is much more elaborate than in locusts: the system is capable of resolving some spatial information, such that an internal representation or template of the horizon is formed. In addition, the system is optimally tuned to movement detection, with an unusually high speed of 2000° s⁻¹. This point, in particular, indicates that this sensory system is designed to support the fast manoeuvres which the dragonfly is able to perform.

Out of a multitude of potential experimental approaches, we selected a behavioural paradigm, determining, by video analysis, the effect that periodic light stimuli exert on the wingbeat timing of animals in tethered flight in a wind tunnel. The wingbeat in locusts and dragonflies is driven by a central oscillator which in turn receives sensory inputs. If we can

show that a periodic visual input, at a frequency close to the flight oscillator frequency, has an effect on its phase, then we know that the bandwidth of the visual component of attitude stabilization is sufficient to exert control at wingbeat frequency.

Once such an effect has been demonstrated, it also becomes possible to determine whether the responses are mediated by the compound eyes or by the ocelli.

General considerations

Limits of time resolution

An initial estimate of the ability of insect sensory systems to exert control of flight at single wingbeat resolution can be derived from a comparison of wingbeat rates and the speed of various sensory systems. The wingbeat periods in flies and bees are in the order of 3 ms, whereas the figure is 20 ms in dragonflies and 50 ms in locusts. The response latencies of mechanoreceptive systems are in the order of 2 ms, thus enabling control at a rate that is adequate for locusts and dragonflies, and marginal for the case of flies. However, mechanoreceptors are subject to drift, and for the detection of absolute cues such as the horizon the usage of visual inputs is necessary. The speed of the ocellar system exceeds that of the compound eyes by a factor of two, an observation that gave rise, in the first place, to the notion that the ocelli are involved in fast attitude corrections. However, even the speed of the ocelli is not necessarily sufficient to resolve single wingbeats: in dragonfly ocellar neurons, the latency between an impulse stimulus and the first sign of a neuronal response is in the order of 8 ms, and it cannot be shorter because it is due to the absolute physical limits arising from the molecular mechanisms of phototransduction. Accordingly, for the case of bees or flies, the time resolution of any visual input is too low for single wingbeat control; in dragonflies the situation is marginal, whereas the speed is adequate in locusts.

Synchronization

As we are examining the interaction between periodic systems, we expect to encounter a phenomenon known as synchronization, whereby a number of oscillators interact in such a way that either oscillator influences the phase and /or frequency of the other. This type of phenomenon has been known for some time but has not yet been used as a tool to study sensory mechanisms.

A flying locust will match its wingbeat frequency to the frequency of a periodical light stimulus, if the frequency of the latter is not too different from the natural wingbeat frequency of the animal (WALDRON 1968). In WALDRON's experiments this coupling occurred because each light flash stimulates the wing elevator motor neurons and/or the wing depressor motor neurons, causing a change of wingbeat phase that was dependent on the temporal relationship between light flash and flight cycle. In the process, the temporal relation between light stimulus and wingbeat changes until it assumes a stable value, meaning that light stimulus and wingbeat assume the same frequency. Furthermore, WALDRON explains that the constant relationship between stimulus and response is stable because the animal makes corrections of small fluctuations in the timing of the flight cycle.

Stimulus and wingbeat constitute two periodical systems that pass through the same phase at regular intervals. The stimulus cycle is composed of alternating dark and light intervals. The flight rhythm is composed of alternating upward and downward strokes of the animal's wings, which may be considered as a sinusoidal movement in first approximation. The flight rhythm is driven by an oscillator in the central nervous system, consisting of a self-excited neuronal network. Even in the absence of any sensory inputs this network will

produce, in two groups of motor neurons, excitation patterns of alternating activity (WILSON 1961). One group innervates the indirect wing depressor muscles, the other innervates the direct elevator muscles, whereby the alternating excitation results in the flight movement (WILSON und GETTRUP 1963, WALDRON 1968). Some insects, including locusts and dragonflies, carry neurogenic, synchronous flight muscles. This means that an action potential in a motor neuron, as triggered by the flight generator, will usually also trigger an action potential in the corresponding muscle, leading to upward and downward wing movements. Thus, the periodic activity of the flight generator directly controls wing movements, via the motor neurons.

Many biological phenomena have endogenous periodic properties, similar to the flight generator of the locust as described above. External stimuli, if they are also periodical, may influence those oscillators and force them to assume a frequency that is dependent on the stimulus (PIKOVSKY et al. 2003). In the above example, the light stimulus represents an independent oscillator, because its frequency is not subject to any inputs from within the system under observation. The flight generator, on the other hand, constitutes a dependent oscillator because it will change frequency in response to external stimuli that act as pacemakers. Such a synchronization or coupling of oscillating systems is known from the level of individual neurons (MOORE et al. 1963) up to complete organisms (ASCHOFF and WEVER 1962).

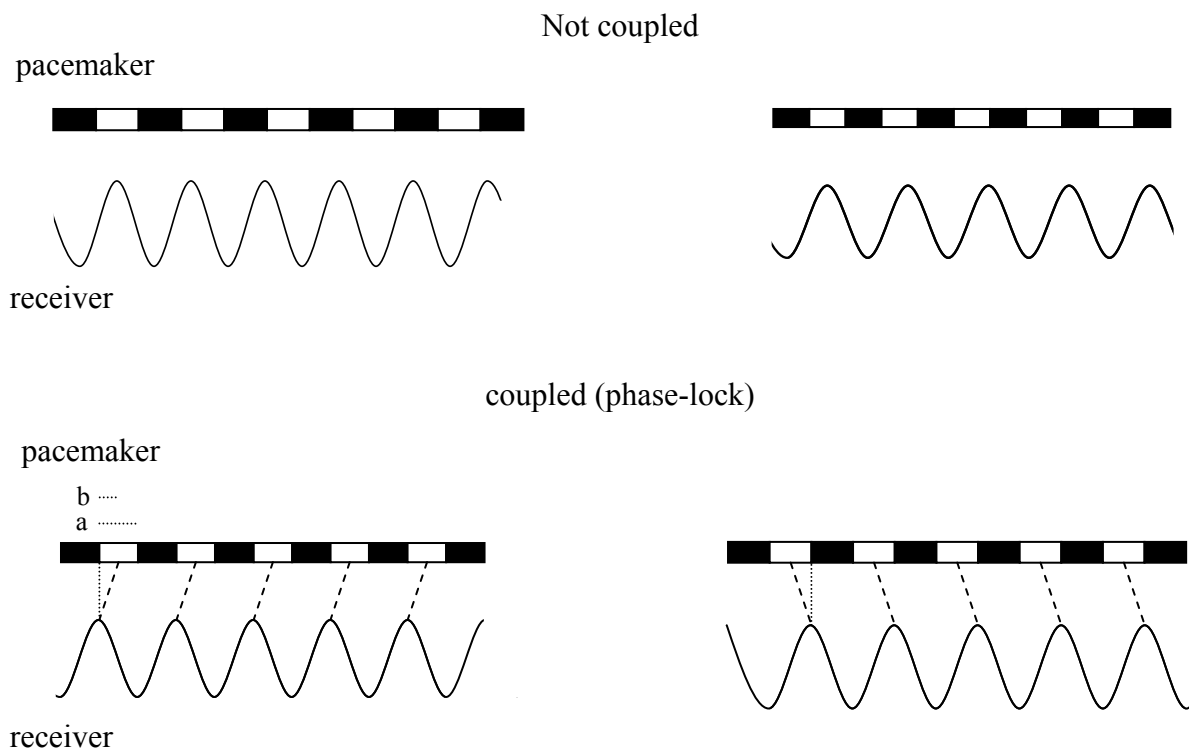


Fig. 1: Effect of frequency differences on the coupling of a dependent oscillator to an independent pacemaker. A periodic light stimulus as an independent pacemaker(upper trace) affects the dependent receiver(lower trace) and causes frequencies to become equal. The phase difference between pacemaker and receiver is defined as the temporal shift between them, as a fraction of total period.

The behavior of a dependent oscillator depends on the strength of the influence of the pacemaker and on whether its frequency was initially higher or lower (CAMHI et al. 1995). This also applies to the synchronization of the flight rhythm of a locust by a light stimulus. If,

for example, the light stimulus is faster than the wingbeat period prior to synchronization, then the wing beat will, after synchronization, always lag with a slight delay. If the light stimulus is initially faster, the phase will lead (Fig. 1). The phase difference (0-1) is defined as the ratio between the time lag and the total period. It is positive or negative, dependent on whether the pacemaker leads or lags the dependent oscillator.

When the dependent oscillator has assumed the same frequency as the pacemaker, the phase difference does not change any more, a condition referred to as phase locking. The magnitude of the phase difference depends upon the conditions prior to synchronization. The more different the natural frequencies are, the greater the phase difference will be. In addition, the phase difference is inversely proportional to the strength of the effect of the pacemaker.

Stimuli that affect the flight generator

The flight rhythm of a locust can be synchronized to several types of external stimuli, for example a forced movement of a single wing (WENDLER 1973), the air current caused by another flying locust (KUTSCH et al. 1994) or, in particular, a periodic light stimulus (WALDRON 1968).

During flight, the central flight generator receives sensory inputs from exteroceptors and proprioceptors. Very important sources are the compound eyes, the wind-sensing hairs on the animal's forehead, the ocelli and internal mechanoreceptors. Information from all of those receptors can be passed from the brain to the flight generator in the thorax by descending interneurons (ROWELL und REICHERT 1986). Some of those interneurons receive direct inputs from the L-neurons of the ocellar nerve, constituting a particularly fast pathway (ROWELL und REICHERT 1986).

Inputs from individual sensory organs may either directly affect the flight rhythm (some ocellar inputs make direct contact to the motor neurons of the pterothorax), or they interact first with other sensory inputs and the flight generator (REICHERT und ROWELL 1985). It also occurs that inputs from e. g. the compound eyes have a secondary effect by first controlling head attitude, followed by separate mechanoreceptive detection of the angle between head and thorax (STANGE 1980).

By interaction with the periodically active flight generator, the reaction strength to those stimuli can be different at different points in the flight cycle, leading to an optimization of the response to the environment (REICHERT und ROWELL 1985, WALDRON 1968, GRISS und ROWELL 1986).

The ocelli

In addition to the compound eyes, many insects also carry 1 – 3 light sensitive ocelli. Ocelli are simple lens eyes and appear to have wide fields of view, because the optics are underfocussed and because many receptor neurons converge upon a small number of second order neurons (L-neurons), turning them into spatial low-pass filters (WILSON 1978). Ocelli are often well developed in flying insects and have been associated with attitude control during flight (REICHERT und ROWELL 1985). They are particularly sensitive to UV (WILSON 1978, STANGE 1981), a wavelength range where the contrast between sky and ground is large.

In laboratory experiments, the ocelli of locusts responded to displacement of an artificial horizon (ROWELL und REICHERT 1986), such that the lateral ocelli were sensitive to displacements around the roll axis, whereas the median ocellus responded to changes in

pitch. Furthermore, ocelli are particularly capable of adapting to darkness: responses to single photons and to small changes in light intensity have been demonstrated (WILSON 1978).

Methods

Animals and preparation

Experimental animals were adult males and females of *Schistocerca gregaria* in their gregarious phase. They were waxed to a holder by their pronotum and mounted in a wind channel.

Experimental setup

An open wind channel of 2.5 m length was used (GEWECKE 1975), generating an air current at 3.5 m/s, heated to 30°C. At its exit opening, diameter 200 mm, the box shown in Fig 2 was attached. It was made of black plastic and open to the rear. At the upper frontal edge an externally synchronizable, firewire-based camera (Basler 602b) was attached. In one of the lower corners a battery of infrared (800 nm) LEDs (Kingsbright BL0307-50-63) was mounted, illuminating the animal but not visible to the camera. Behind the animal a red digital display was mounted, visible to the camera but not to the animal.

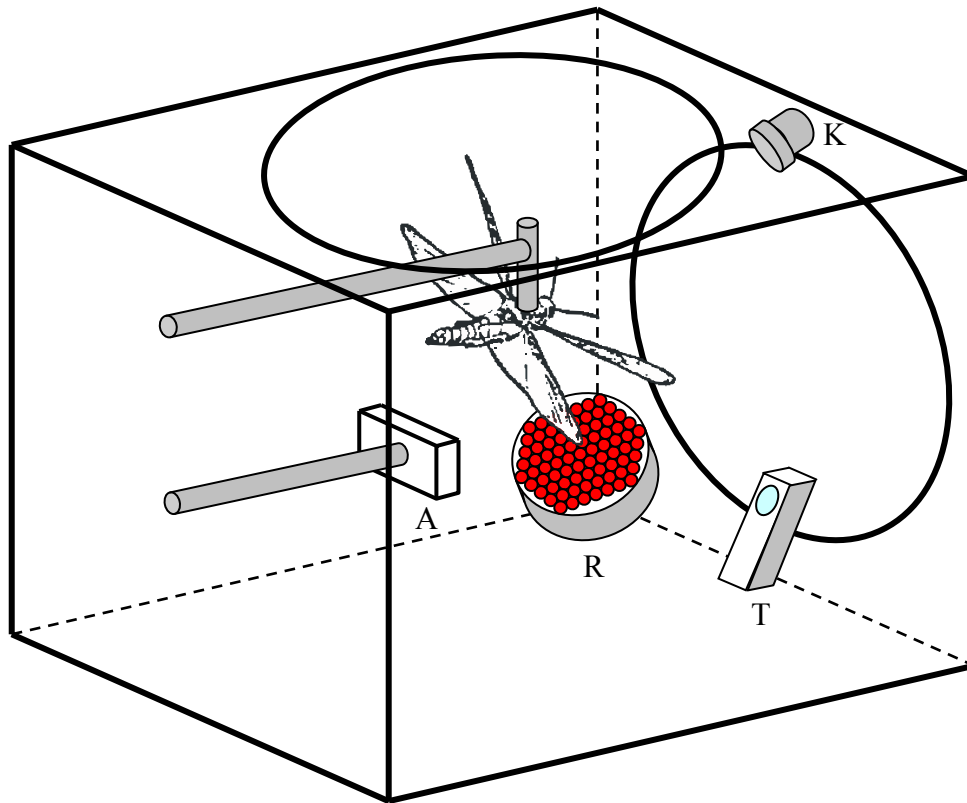


Fig. 2: Schematics of experimental setup. The animal is mounted in the centre of the box, with a digital display (A) behind it, at an oblique angle. The animal is illuminated by an infrared LED array (R) and is within the field of view of a digital camera (K). Another LED (T) is used to present light stimuli to the animal. A circular opening at the front admits the air current, and scattered light is admitted through an opening from above. To the rear, the box is open.

At the lower edge of the entry side of the box the light stimulator was located, consisting of an UV LED (380 nm; $2.16 \cdot 10^{15}$ photons / cm²) angebracht. This LED was located 90 mm below the plane of the animal, from where it is visible to both compound eyes and ocelli. This

position, extending by approximately 10 mm into the air current, was chosen to minimize turbulence.

The digital display and the camera trigger input were connected to the output of a custom-designed pulse generator, and so were the stimulus LED as well as an oscilloscope for monitoring purposes. The infrared LED array was driven by 10 V DC via a 15 Ω resistor. The circular aperture above the animal was covered by a polarization filter and diffuser, illuminated by a 16 W incandescent globe. This source was devoid of UV but its presence improved flight behaviour.

Experimental procedure

The animal was positioned at the centre of the box, facing upwind. Flight activity could be evoked by removing ground contact by the feet in combination with an air current, heated to 30°C, with a speed of 3.5 m/s.

During the first half of each stimulus period, the LED was normally not switched on; in the second it was, and after the dark/light transition the camera took an image with an exposure time of 0.5 ms. This sequence could be reversed by a switch (Fig 3). The digital display was always darkened during the first half of the stimulus period, while an associated clock/counter measured the stimulus duration with a resolution of 0.1 ms. In addition, the decimal point to the left of the most significant digit (Fig. 5) was lit if the image was taken during the light-on phase. Stimulus duration was always measured during the first half-period and displayed during the second. The position of the left forewing was used to assess the animal's reaction.

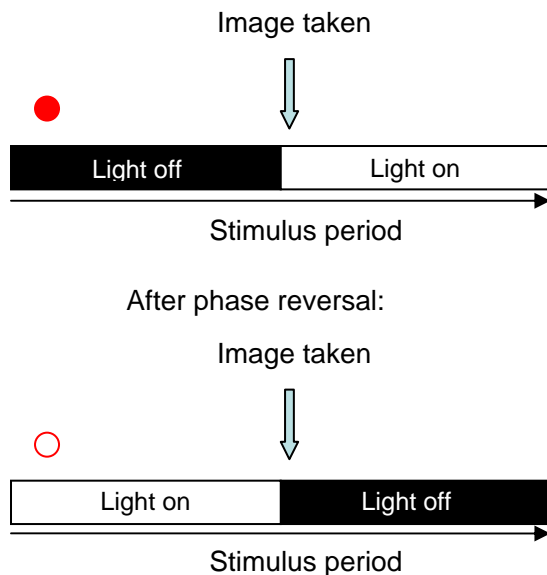


Fig 3: Temporal relationship of stimulus LED and camera. The sequence of light and dark phase can be reversed. The camera always takes an image at the second half of the stimulus period. If the image is taken in the light phase, a marker dot on the display is activated.

In this arrangement, the camera and the UV-LED are the equivalent of a stroboscope. If wingbeat and camera are of the same frequency, the wing will be in the same position for every image and hence appear to be stationary. For different frequencies the wing will be in different positions in sequential images, appearing to move in the recording, at a frequency that equals the frequency difference. Images were digitized using the firewire capture software by Ultravision and could be observed in real time. Frame capturing was buffered in memory such that interesting sequences could be saved after observation.

The UV LED as the dominant pacemaker

Using the pulse generator, the frequency of image and stimulus was varied by hand until it was identical to the wing beat frequency of the animal. This was recognizable by an apparent standstill of the wing on the capture display. As the frequency ratio was close to unity at the outset, this means that one full wingbeat cycle has taken place between two subsequent images.

Once such a stable condition was achieved, the phase of the light stimulus was reversed. If this resulted in a transient wing movement, towards a new stable condition, it was concluded that a response to the modified stimulus had occurred, as the switching of the stimulus was the only condition that had changed. The occurrence of such a response also demonstrated that the equality of frequencies was not by coincidence.

The range of synchronization

Furthermore, a test was designed for the frequency range over which the animals can follow the pacemaker. First, the stimulus generator was adjusted to match the wing beat frequency. This was followed by modulating the stimulus frequency by a triangle waveform of 20 s duration (Fig. 4) and adjustable amplitude which was applied for several of its periods.

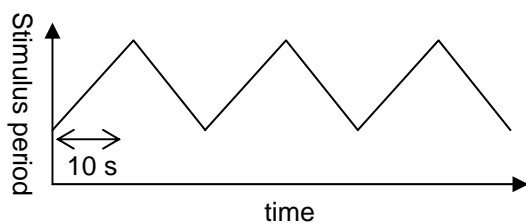


Fig. 4: Modulation of stimulus frequency over a defined range.

Analysis of recordings

Using MatLab (Version 7.1.0.246 [R14] Service Pack 3), the recorded videos were analysed frame by frame, marking the wing position in each frame. The corresponding stimulus period was read off the image of the display, and so was the status of the marker that identified stimulus phase. For further analysis, data were exported to Microsoft Excel 2003.

Selected results

I. Locusts

Flight behavior

In all animals that could be induced to fly steadily, it was possible to lock, at least temporarily, the wingbeat frequency to the camera/stimulus frequency. On the screen, the wings then appeared to stay still, although direct observation showed them to be moving. Duration and stability of the locking varied, the longest locking period being 30 s (Fig. 6). When images were taken in the dark phase, the forewing was usually in a lowered position, whereas it was usually in a raised position for recordings in the light phase (Fig. 5). However, there were repeated but brief episodes where the wing would appear to freeze in an intermediate position.

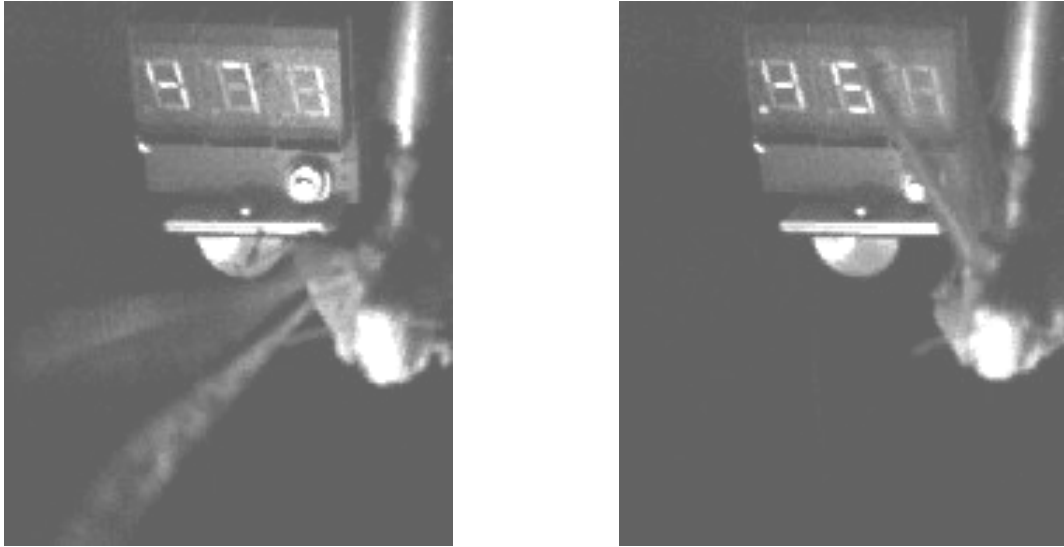


Fig. 5: Phase-lock of wingbeat frequency. In the images, the forewing appears to be stationary, either in a lowered position (left, image during dark phase) or in a raised position (right, image during light phase). Both recordings are from the same experiment.

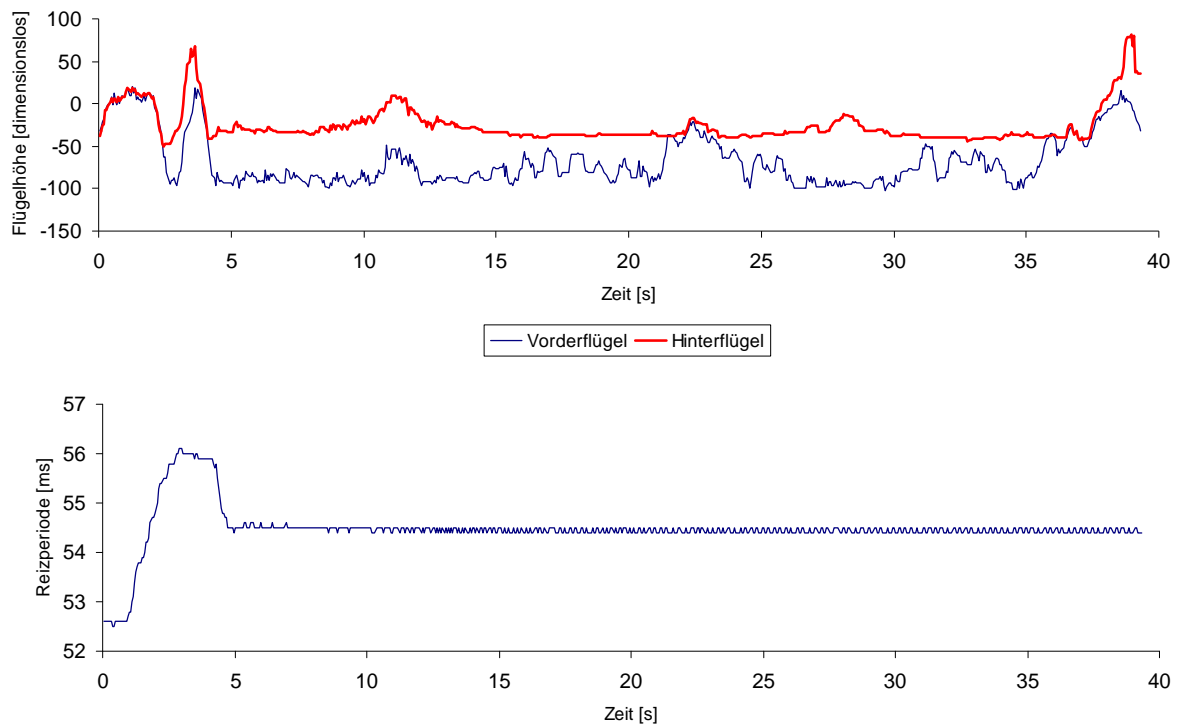


Fig. 6: Phase locking of wingbeat and light stimulus. Top: the positions of forewing (blue) and hindwing (red) remains the same, with slight fluctuations, while the stimulus frequency is kept constant (bottom). Phase locking commences after 5 s and lasts for another 20 s.

In addition to showing the position of the forewings, Fig. 6 also shows the position of the hindwings. Here, as in all other recordings, the response of the hindwings is similar to that of the forewings. For the intervals from 5 and 10 s and from 14 to 20 s the consistently lowered wing position is superimposed by periodic variations whose origin remains to be identified.

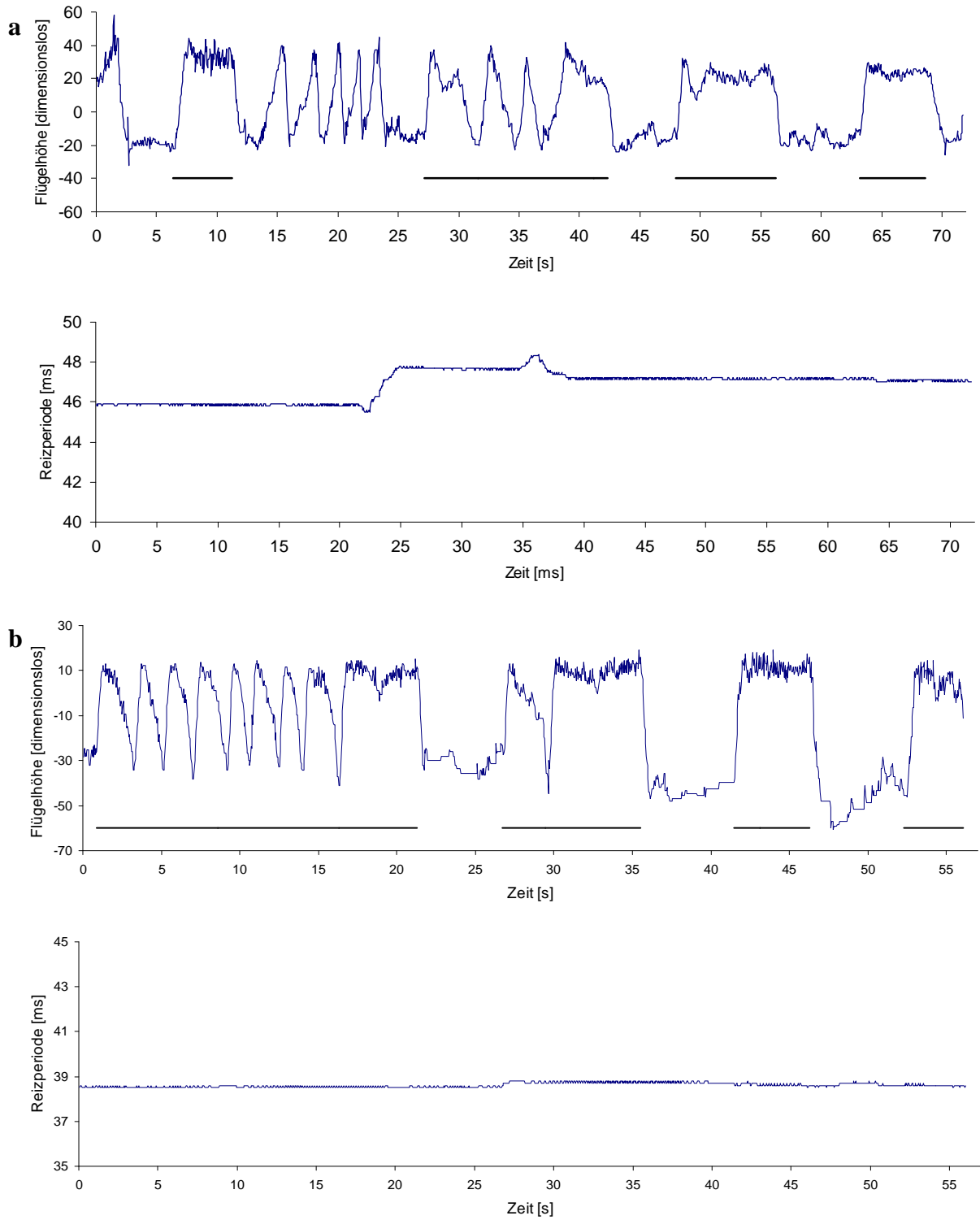


Fig. 7: (a) Top: wing position as a function of time, in response to stimuli at the periods shown in (b), and in response to changes in stimulus phase (black bars mark that light-on and recordings are in phase, their absence marks opposite phase. (b) same, from different animal.

The UV LED as the dominant pacemaker

The reversal of light and dark phase would cause, in all animals and most of the times tested, a sustained change of wing position in the stroboscopic images. In the optimal case,

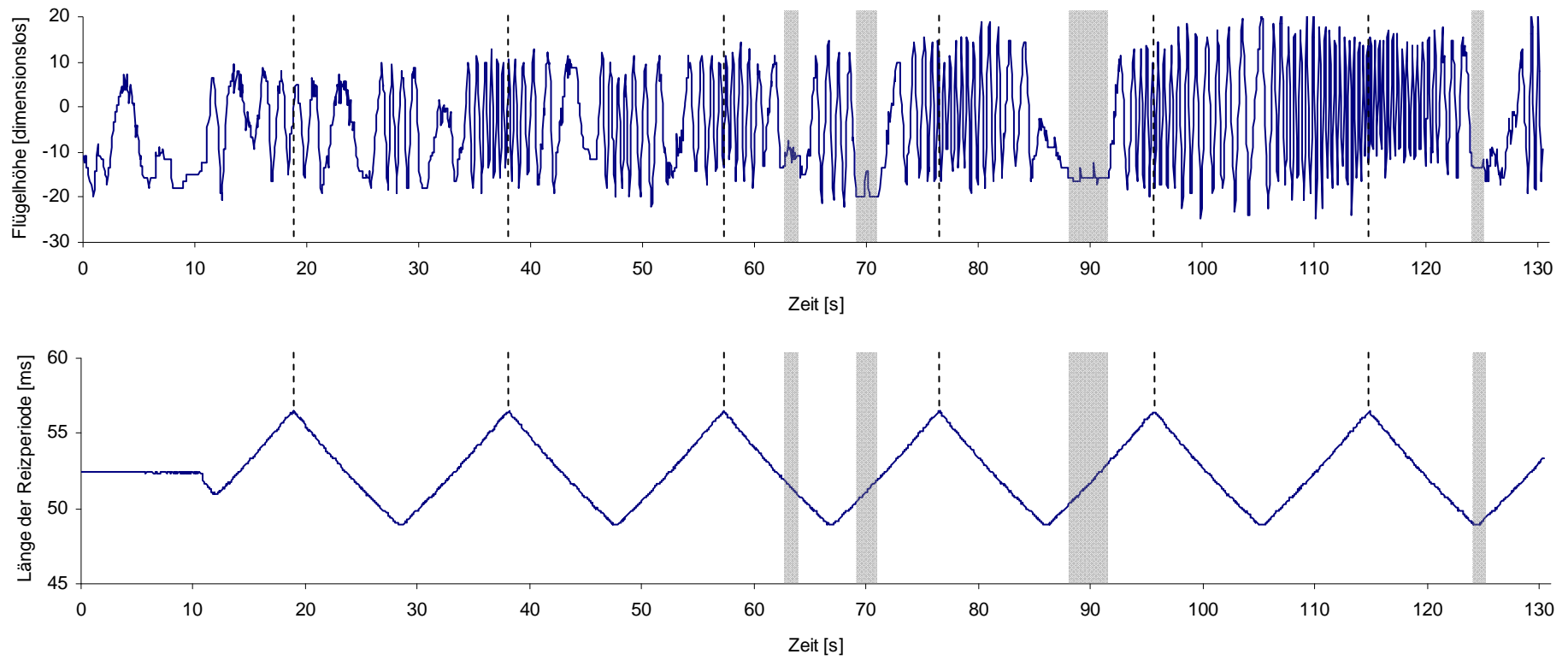


Fig. 8: Changes of wingbeat frequency with a continuously swept stimulus period. The wing position (top) can be captured by the pacemaker (bottom) over a certain range (grey bars). A stationary wing implies phase locking. Elsewhere, the apparent frequency of the movement equals the difference frequency between stimulus and wingbeat.

the wing position changes from a stable raised to a stable lowered position or vice versa (Fig. 7).

After phase reversal it may sometimes happen, however, that the animal temporarily loses synchronization, appearing as several apparent wing beats in the recordings. However, a return to a stable position would occur eventually. Both the animals presented in Fig. 7 show such episodes.

The range of synchronization

Fig. 8 shows the wing position of an animal during sweeps of stimulus frequency. When the difference between stimulus frequency and wing beat frequency is large, the wing appears to move rapidly. As the frequencies approach each other, the apparent movement of the wing slows down until a stable position occurs, for which the wing beat frequency may lock onto the stimulus frequency, while the latter keeps changing. In Fig. 8, such episodes are marked in grey. In particular at $t = 90$ s it is obvious that capture has occurred for a considerable range of stimulus periods. The capture range is essentially similar in subsequent sweeps although there are considerable variations in the strength of the effect. In the recording of Fig. 8 phase locking was not evident during the first half: although the frequencies approach each other, resulting in an apparent slowing down of the wing beat, no stable synchronization was observable.

Thus it appears that transient capture and phase locking by a frequency modulated stimulus does occur, but the effect is tenuous for the rate of frequency change that was used in this set of experiments. A more targeted approach, using a slower rate of frequency change, will be possible in further experiments.

Compound eyes or ocelli?

In order to identify the part of the visual system that drives the synchronization responses, the median ocellar nerve were cut in 3 animals and the compound eye optical tracts were cut in a further set of 3 animals. All animals could be made to fly in the wind tunnel, and the result is unequivocal: animals with an intact median ocellus and severed compound eyes continue to exhibit phase locking, whereas phase locking is absent in animals with a severed median ocellus and intact compound eyes.

II. Dragonflies

Experiments that were identical to those described above were also performed on dragonflies. In no case was it possible to reliably identify phase locking. We observed that dragonflies never show the prolonged periods of steady flight that are common in locusts, but rather switch frequently between different patterns of wing beat, of which there are several available to dragonflies. It is possible that this switching has been masking any evidence for phase locking. As it has also come to our attention that Hisada et al. (1965) report that stability of the frequency of wingbeat was tested by stimulating the eyes with stroboscopic flashes and that no apparent correlation was found, we conclude that the phase locking phenomenon is either absent or experimentally not accessible in dragonflies.

Discussion

We have demonstrated that phase locking of wing beat rate by an UV light stimulus can be reproducibly evoked in locusts. So far, the best demonstration is given by manually matching the pacemaker frequency to wingbeat frequency and then evoking a phase reversal of wing position by phase reversal of the stimulus. There is also a reproducible effect in response to regular frequency modulation of the stimulus: an episode of rather stable synchronization, for a change of period of 3 ms and covering a timespan of 5s, is shown in Fig. 8. However, there is ample space for refinement and expansion of this experiment.

The observation of phase locking is consistent with old observations, taken nearly 40 years ago; the novelty of our findings lies in the fact that the older work was directed at the mechanisms of entrainment of periodic phenomena *per se*, whereas we use the phenomenon as a tool to examine the limits of time resolution of the visual system, within the context of flight control.

We find that the phenomenon is evoked via the median ocellus and not the compound eyes. This is consistent with the idea that the speed advantage of the ocelli due to their more direct wiring is crucial to their function. The absence of an effect in dragonflies might imply that their wingbeat frequency (50 Hz) is outside the bandwidth of even the ocellar system, whereas the wingbeat frequency of locusts (22 Hz) is within that bandwidth.

Thus, the lesson for the design of flapping wing MAVs is that locusts with wing beat at 22 Hz can use feedback from a vision-based external reference frame for the stabilization of wingbeat, whereas insects with higher wingbeat rates, namely not only dragonflies, but also bees and flies, can do without it. From this, it follows that the scaling of pitch oscillation modes on the one hand, and the scaling of wingbeat frequency on the other, as a function of size, is worth comparing. It may be that the coupling between wingbeat and longitudinal oscillatory modes, as suggested by TAYLOR and THOMAS (2003) is relevant to flapping wing craft down to the size of locusts but not below. Interestingly, Sun and Xiong (2005) report that the hovering flight of the bumblebee is dynamically unstable, due to an unstable oscillatory mode. However, they suggest that this instability might not be a great problem to a bumblebee that tries to stay hovering: the time for the initial disturbances to double (0.1 s) is more than 15 times the wingbeat period (6.4 ms), and the bumblebee has plenty of time to adjust its wing motion before the disturbances grow large.

The question might be posed as to what extent phase locking by light stimuli is not just a useful tool, but is directly relevant to flight control. It is difficult to conceive why it should make sense for a locust to match its wingbeat frequency exactly to a periodic light stimulus. However, on the other hand, it is quite easy to conceive that there is a periodic light stimulus that is actually caused by wingbeat: the ocelli are quite sensitive to the changes of light intensity associated with displacements of the horizon, including those that are caused by the animal being rocked by its own moving wings. An interaction between light stimuli and wing beat frequency within the context of flight control was demonstrated by ROWELL and REICHERT (1986). If, during our experiments, the periodic changes of light intensity are indeed

interpreted as a wobbling horizon, the animal will continuously attempt to apply corrections. This could be the explanation for phase locking.

Furthermore, it is possible that phase locking is relevant within the context of swarm behaviour. Camhi et al. (1995) showed that locusts flying in tandem could lock their flight frequencies, via wind detectors as the sensory inputs. It might be that the modulation of light intensity by the wingbeat of neighbours close to an animal has a similar effect.

References

- ASCHOFF, J., WEVER R. (1962): Über Phasenbeziehungen zwischen biologischer Tagesperiodik und Zeitgeberperiodik. *Zeitschrift für vergleichende Physiologie*. **46**, 115-128
- CAMHI, J.M., SUMBRE, G., WENDLER, G. (1995): Wing-beat coupling between flying locust pairs: preferred phase and lift enhancement. *J. Exp. Biol.* **198**, 1051-1063
- DUDEL, J., MENZEL, R., SCHMIDT, R. F. (1996): Neurowissenschaft – Vom Molekül zur Kognition. *Springer Verlag*. Berlin, Heidelberg, New York. pp. 185
- GEWECKE, M. (1975): The influence of the air-current sense organs on the flight behaviour of *Locusta migratoria*. *J. Comp. Physiol.* **103**:79–95
- GRISS, C., ROWELL, C.H.F. (1986): Three descending interneurons reporting deviation from course in the locust. I. Anatomy. *J. comp. Physiol. A*. **158**, 765-774
- HISADA, M., TAMASIGE, M., SUZUKI, N. (1965): Control of the flight of the dragonfly *Sympetrum darwinianum* Selys. I Dorsophotic response. *J. Fac. Sci. Hokkaido Univ. Ser. VI, Zool.* **15**, 568-577
- HOLST, E. von (1939): Die relative Koordination als Phänomen und als Methode zentralnervöser Funktionsanalyse. *Ergebn. Physiol.* **42**, 228-306
- KUTSCH, W., CAMHI, J., SUMBRE, G. (1994): Close encounters among flying locusts produce wing-beat coupling. *J. Comp. Physiol. A* **174**, 643-649
- MIZUNAMI, M. (1995): Functional diversity of neural organisation in insect ocular systems. *Vision Res.* **35**, 443-452
- MOORE, G. P., PERKEL, O. H., und SEGUNDO, J. P. (1963): Stability patterns in interneural pacemaker regulation. *Proc. Of San Diego Symposium for Biomedical Engineering*, 184-193
- PIKOVSKY, A., ROSENBLUM, M., KURTHS, J. (2003): Synchronisation – A universal concept in nonlinear sciences. *Cambridge University Press*.
- REICHERT, H., ROWELL, C.H.F. (1985): Integration of nonphaselocked exteroceptive information in the control of rhythmic flight in the locust. *J.*

Neurophys. **53**, 1201-1218

ROWELL, C.H.F., REICHERT, H. (1986): Three descending interneurons reporting deviation from course in the locust. II Physiology. *J. comp. Physiol. A.* **158**, 775-794

STANGE, G. (1981): The ocellar component of flight equilibrium control in dragonflies. *J. comp. Physiol.* **141**, 335-347

SUN, M, XIONG, Y. (2005): Dynamic flight stability of a hovering bumblebee. *J. Exp. Biol.* **208**, 447-459

TAYLOR, G. K., THOMAS, A. L. R. (2003): Dynamic flight stability in the desert locust *Schistocerca gregaria*. *J. Exp. Biol.* **206**: 2803-2829

WALDRON, I. (1967): Neural mechanism by which controlling inputs influence motor output in the flying locust. *J. Exp. Biol.* **47**, 213-228

WALDRON, I. (1968): The mechanism of coupling of the locust flight oscillator to oscillatory inputs. *Z. Vergl. Physiol.* **57**, 33-347

WENDLER, G. (1974): The influence of proprioceptive feedback on locust flight coordination. *J. Comp. Physiol.* **88**, 173-200

WILSON, D. M. (1961): The central nervous control of flight in a locust. *J. Exp. Biol.* **38**, 471-490

WILSON, D. M., GETTRUP, E. (1963): A stretch reflex controlling wingbeat frequency in grasshoppers. *J. Exp. Biol.* **40**, 171-185

WILSON, D. M., WEIS-FOGH, T.(1962): Patterned activity of co-ordinated motor units, studied in flying locusts. *J. Exp. Biol.* **39**, 643-667

WILSON, M. (1978): The functional organisation of locust ocelli. *J. Comp. Physiol.* **124**, 297-316